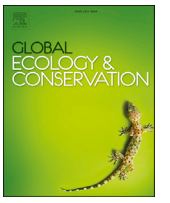
Global Ecology and Conservation 24 (2020) e01240

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco



Original Research Article

The importance of genetic diversity for the translocation of eight threatened plant species into the wild

Deborah Schäfer [a, b, *, 2], Hugo Vincent [a, 2], Markus Fischer [a, b, 1], Anne Kempel [a, c, 1]

[a] University of Bern, Institute of Plant Sciences, Altenbergrain 21, 3013, Bern, Switzerland
[b] Botanical Garden of the University of Bern, Altenbergrain 21, 3013, Bern, Switzerland
[c] Oeschger Centre for Climate Change Research (OCCR), Hochschulstrasse 4, 3012, Bern, Switzerland

ARTICLE INFO

Article history:
Received 6 January 2020
Received in revised form 18 August 2020
Accepted 18 August 2020

Keywords:
Conservation biology
Nature conservation
Reintroductions
Introductions
Multi-species experiment

ABSTRACT

Considering ongoing biodiversity losses, translocations of threatened plant species into the wild has become a common conservation technique although they are considered laborious, expensive and rarely successful. It is broadly accepted that the choice of suitable translocation sites and the translocation of many individuals increase their success. Moreover, high genetic diversity among introduced plants is suggested to be important but has been rarely assessed for populations of threatened species. Here, we tested whether higher genetic diversity generally increases early establishment of threatened plant species after a translocation. We translocated plantlets of eight rare and threatened species of Switzerland at one apparently suitable site per species. We planted 40 to 312 plants per site at two levels of genetic diversity, monoculture plots with offspring of single seed families per species, and mixture plots with offspring of several seed families per species. In the early translocation stages, plots with individuals of several seed families had a higher survival than plots with individuals of only one seed family, however, the positive effect of diversity disappeared with time. Our study suggests that a high genetic diversity is important at least for the short-term survival of translocated populations of threatened plant species. Translocations should therefore always aim to maximise genetic diversity in founder populations. Experimental approaches as the one we present here are important tools to realise long-term translocation experiments that are needed to enhance our understanding of the underlying factors responsible for success or failure of translocations of threatened plant species. We therefore recommend close collaborations between experimental plant ecologists, field botanists and conservation practitioners in future translocations of threatened species.

© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

* Corresponding author.
E-mail address: deborah.schaefer@boga.unibe.ch (D. Schäfer).
[1] equally contributing last authors.
[2] equally contributing first authors.

https://doi.org/10.1016/j.gecco.2020.e01240
2351-9894/© 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Species diversity has been lost at an unprecedented rate (Dirzo and Raven, 2003; Taberlet et al., 2012). Habitat loss and fragmentation are the greatest drivers of the rapid decline in biodiversity (Sala, 2000; IPBES et al., 2018) and measures to prevent further biodiversity loss have received considerable attention. Among those, habitat protection and restoration are the most important and most commonly used conservation methods (Maunder, 1992; IUCN, 2014). For threatened plant species, however, habitat protection and management are often insufficient, and translocations, i.e. the deliberate release of organisms in a natural habitat (Wolf et al., 1996; Weeks et al., 2011), have become an essential conservation technique (Vergeer et al., 2004; Menges, 2008; IUCN, 2014).

Translocations aim to ensure the long-term survival of threatened species, either by reinforcing the size and genetic diversity of present populations, or by creating new self-sustaining populations in suitable habitats (Wolf et al., 1996; Menges, 2008; Weeks et al., 2011). Despite their broad acceptance as an important tool to overcome dispersal limitation (Vergeer et al., 2004) and to complement in situ conservation measures (IUCN, 2014), their use is discussed controversially as they are labour-intensive, expensive and often unsuccessful (Maunder, 1992; Godefroid et al., 2011; Drayton and Primack, 2012; Maschinski et al., 2012). Many factors can affect the success of rare plant species translocations, including the choice of a suitable habitat (Noël et al., 2011), the number and type (e.g. seeds, plants) of propagules introduced (Frankham et al., 2010) and the origin and genetic diversity of these propagules (Price and Waser, 1979; Menges, 2008; Maschinski et al., 2012). So far the relative importance of these factors for translocations is unclear and not equally well studied.

Many studies underline the importance of high genetic diversity for the fitness and survival of natural populations (Oostermeijer et al., 1994; Fischer and Matthies, 1998). High genetic diversity increases the chance of having pre-adapted genotypes to future perturbations (Gamfeldt and Källström, 2007). It can also lead to complementarity between different genotypes of a single species, i.e. increased fitness of individuals from different maternal plants due to e.g. resource partitioning caused by different traits (Loreau and Hector, 2001), or it may decrease the impact of enemies such as herbivores or pathogens (Zhu et al., 2000; Tooker and Frank, 2012). Finally, a high genetic diversity increases the probability of a population to adapt to changing environmental conditions (Mayr, 1963; Ouborg and van Treuren, 1994; Jump et al., 2009; Weeks et al., 2011) and reduces inbreeding levels and thus the expression of inbreeding depression (Charlesworth and Charlesworth, 1987; Ellstrand and Elam, 1993; Godt et al., 1996; Krauss et al., 2002; Ottewell et al., 2016). Therefore, high genetic diversity might be crucial for successful translocations (Lesica and Allendorf, 1999; Vergeer et al., 2005; Prati et al., 2016; Ottewell et al., 2016). There are for example studies that tested the influence of the size of the source populations on seed fitness and germination (Godefroid et al., 2016), how multi-source translocations can be beneficial due to increased genetic diversity (Zavodna et al., 2015) and how the fitness of offspring can be increased by outcrossing (Barmentlo et al., 2018). There is, however, only limited experimental evidence for the positive effect of genetic diversity on single-source translocations of threatened species, which often have reduced levels of genetic diversity due to low or declining population sizes (Gaston, 2006). Such single source populations are still often performed in conservation practice, as source material is often rare (personal communication with *Info Flora*, National Data and Information Centre on the Swiss Flora). A few experimental studies showed that translocations of individuals of several seed families (i.e. seeds originating from different maternal plants) of *Arnica montana* had increased survival compared with translocations of individuals of only one seed family (Vergeer et al., 2005). Moreover, reintroductions of several genotypes of the clonal *Ranunculus reptans*, a rare plant species of Switzerland, were more successful than reintroductions of only single genotypes (Prati et al., 2016). Further, in a meta-analysis, Forsman (2014) found strong evidence of increased establishment success in plants and animals with higher levels of genetic and phenotypic diversity. However, of the nine studies on plants included in this meta-analysis only seven were performed in natural conditions and none of these studies translocated rare or threatened plant species. Therefore, it remains unclear whether it is a general pattern that high genetic diversity increases translocation success of rare and threatened plant species in natural conditions.

In Switzerland, 30% of the species-rich flora are considered threatened (Moser et al., 2002; Bornand et al., 2016). Based on a large database on plant records (Bornand et al., 2016) and comprehensive knowledge on species characteristics and requirements of plants native in Switzerland (Landolt and Bäumler, 2010), a list of priority species for conservation was established, taking into account the degree of threat and the responsibility Switzerland has at a global level to preserve a particular species (FOEN, 2011). For this study, we selected eight rare and threatened plant species from this priority list, originating from different habitats and plant families (Table 1). We then grew seedlings from field-collected seeds and performed translocations with plantlets into wild habitats. For each species, we introduced plants at two levels of genetic diversity by either planting offspring of only single maternal plants (monoculture plots) or offspring of different maternal plants (mixture plots) and compared their survival, plant height and the number of flowering individuals in the first two years. With this design, the main goal was to test the fundamental question whether increased genetic diversity enhances the early establishment of translocated populations of threatened plant species. Further, we monitored the translocations for four years to assess the potential of creating viable populations of such rare species on the short term.

Table 1
Study species. Study species with their plant family, IUCN category of threat (VU: vulnerable, EN: endangered, CR: critically endangered, Red List of Switzerland, Moser et al., 2002), priority for conservation in Switzerland (1: very high, 2: high, 3: moderate, 4: low; List of National Priority Species, FOEN, 2011), their habitat preference (Lauber et al., 2012) and a selection of important life-history traits (Landolt et al., 2010).

Species	Plant family	Red list status (CH)	Priority (CH)	Habitat	Growth form	Vegetative propagation	Mating system & pollination
Allium angulosum	Amaryllidaceae	VU	4	Wet meadows	Geophyte	Bulbs & basal lateral shoots	Self-pollination & insect pollination
Campanula cervicaria	Campanulaceae	EN	3	Clay soils in shady places, changing soil humidity	Hemicryptophyte	No vegetative dispersal	Insect pollination
Cleistogenes serotina	Poaceae	VU	4	Dry grasslands	Hemicryptophyte	Below-ground runners	Wind pollination
Inula helvetica	Asteraceae	VU	2	Often next to bushes along water and at forests edges	Hemicryptophyte	Below-ground runners	Cross-pollination
Ludwigia palustris	Onagraceae	CR	2	Trenches, at the margins of ponds, occasionally flooded	Hemicryptophyte	Parts breaking off & creeping shoots	Self-pollination & insect pollination
Oenanthe lachenalii	Apiaceae	CR	2	Wet grasslands	Geophyte	Basal lateral shoots	Insect pollination
Senecio erraticus	Asteraceae	EN	3	Along moist forest paths, brooksides, and alluvial soils	Hemicryptophyte	Basal lateral shoots	Insect pollination
Teucrium scordium	Lamiaceae	EN	3	In fens, in trenches, and on river banks	Hemicryptophyte	Below- & above-ground runners	Cross-pollination

2. Material and methods

2.1. Study species and study sites

In 2011 and 2012 seeds of the eight selected rare plant species of conservation priority in Switzerland (Table 1, Moser et al., 2002; FOEN, 2011) were collected from single natural populations. The seeds were harvested from 10 to 20 maternal plants per species. The maternal plants were located at least 5 m apart from each other and covered the whole area of the population. The seed families (i.e. seeds originating from the same maternal plant) were stored separately. In spring 2013, we sowed the seeds (separated by species and seed family) in germination trays. The seedlings were then transplanted into pots (diameter 9 cm) filled with normal potting soil (Ricoter, Aarberg, Switzerland) and placed in a common garden (Botanical Garden of the University of Bern, Switzerland). Between July and October 2013 we transplanted each species into a separate natural site (Table A1). We selected the translocation sites for each species in collaboration with expert botanists and local conservation practitioners who know the habitats, the species and the existing populations to minimize geographical distance and to maximise ecological similarity with the source populations and to ensure suitable management for the individual species.

2.2. Study design

We defined two levels of genetic diversity: monoculture plots (each with individuals of a single seed family) and mixture plots (with individuals of several seed families). With this approach we aim to answer the fundamental question of whether a high genetic diversity is important for the short-term translocation success, similar to proof of concept studies in biodiversity ecosystem functioning research (Zeng et al., 2017). The reader should be aware that translocations for conservation practice should always be conducted with offspring from many seed families (see guidelines for Switzerland and from the IUCN, https://www.infoflora.ch/de/flora/ansiedlung/ansiedlung.html; IUCN, 2013). We planted n (n = number of seed families per species, ranging from 5 to 13) monoculture plots and n mixture plots per species. Each monoculture plot consisted of n-1 individuals of one seed family. Each mixture plot consisted of a unique combination of n-1 individuals of different seed families (Fig. 1, see Table A2 for more information on the translocation design for each species). We planted the individuals at 20 cm distance within plots and with 40 cm distance between plants of different plots. With the distance of 40 cm between individuals of different plots, we ensured to have no direct interactions between individuals of different plots in the first two seasons after the translocations. The monoculture and mixture plots were alternated to consider possible underlying not

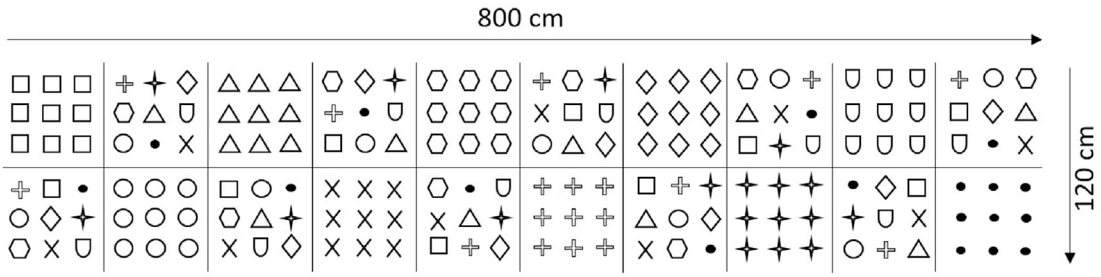


Fig. 1. Design of the translocation plots. Example: *Allium angulosum* (180 individuals, 10 seed families, 10 monoculture plots, 10 mixture plots). Each entry represents one individual plant and each symbol represents one seed family.

visible gradients of abiotic conditions. All plants were planted in the existing vegetation and were watered immediately after planting. Next to the normal site management suitable for the respective species, no additional care was provided thereafter.

2.3. Measurements

Two months after the translocations (1st season), and in spring 2014 (seven to ten months after the translocations, 2nd season), we recorded plant survival, measured the height of the introduced plants as a non-destructive estimation of plant performance, and recorded whether plants were flowering. Flowering could only be analysed for *Ludwigia palustris* and *Oenanthe lachenalii* in the 2nd season, as the other species had not flowered yet or at very low numbers. In the 1st season, individuals from three species were too small to be measured with the same precision as the other species. Thus, we did not record plant height for these species at this stage.

In autumn 2015 (two years after the translocations, 3rd season) and in autumn 2016 (three years after the translocations, 4th season) we monitored the translocated populations again. As only the plots but not the individuals themselves were marked, mortality of individuals and the production of offspring by sexual reproduction or vegetative propagation prohibited us from identifying the originally planted individuals unequivocally. Therefore, we refrained from assigning the plants to their respective seed families or treatments at this stage. For each species, we counted the number of individuals, calculated population performance as the number of individuals divided by the number of individuals planted, and also counted the total number of flowering individuals.

2.4. Statistical analysis

To test whether plant performance was affected by genetic diversity, we used generalized linear mixed effect models (*glmer*) with a binomial error distribution for the survival and flowering data and linear mixed effect models (*lmer*) for the continuous plant height data (package lme4, Bates et al., 2015). We tested for the effect of genetic diversity after the 1st season and after the 2nd season. Plant height for dead individuals was set to NA to only look at the diversity effect on surviving individuals. The models included treatment (monoculture plot, mixture plot) as fixed effect, and species, seed family, and plot identity as random factors. We also included the time since transplantation (in days) as a covariate. We additionally carried out the analyses for each species separately, where we only included seed family and plot identity as random factors. We log-transformed plant height to account for non-normal distribution. Examples of the code for survival across all species and for the individual species can be found in Appendix A3.

The effect of the diversity treatment could not be analysed beyond the 2nd season (see above), as we were not able to assign the individual plants to their original treatment any longer. The data of the 3rd and 4th season therefore only serves as a measure of population performance of our translocations in the longer run. We calculated population performance as the number of individuals counted in relation to the number of individuals planted.

All data were analysed using R, Version 3.3.2 (R Core Team, 2016).

3. Results

3.1. Effect of genetic diversity over all species

During the 1st season, over all species survival was by 5% higher in the mixture plots than in the monoculture plots ($p = 0.03$), while plant height was not affected by the genetic diversity treatment (Fig. 2a,c, Table 2). By the 2nd season overall species survival (Fig. 2b) and plant height (Fig. 2d) did not differ between mixture and monoculture plots (Table 2).

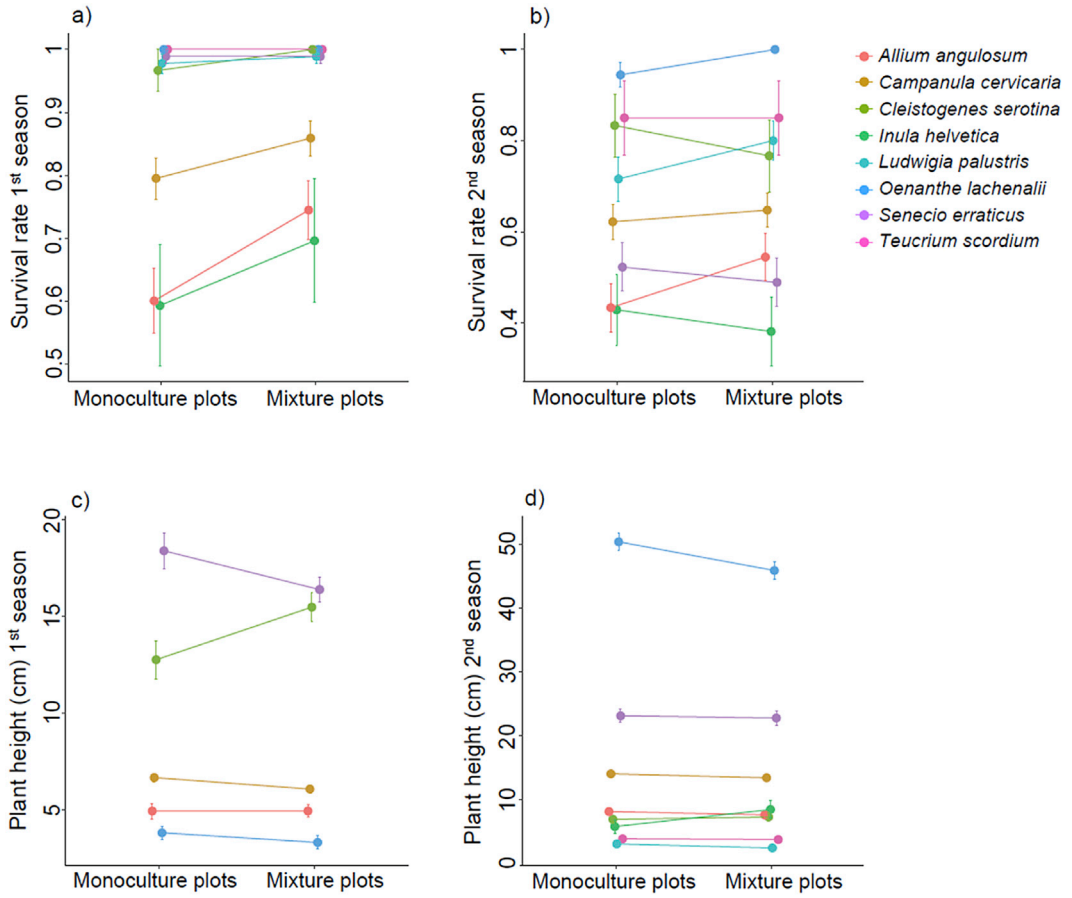


Fig. 2. Overview of effects of genetic diversity. Effects on a) survival rate for the 1st and b) 2nd season in relation to the number of planted individuals, and c) plant height for the 1st and d) 2nd season of all eight plant species in monoculture plots (individuals of one seed family) and mixture plots (individuals of several seed families). Plotted values are the calculated means of the raw data, bars indicate the standard errors.

3.2. Effect of genetic diversity on individual species

Analysing each species separately, we found few differences in survival and plant height between monoculture and mixture plots. During the 1st season, individuals of *Allium angulosum* tended to survive better in the mixture plots ($p = 0.07$, Fig. 3a, Table 2). Individuals of *Cleistogenes serotina* were taller when growing in the mixture plots ($p = 0.03$, Fig. 3b, Table 2). However, for both species, these effects were transient and disappeared later. In the 2nd season, individuals of *Inula helvetica* tended to be taller in the mixture plots ($p = 0.10$, Fig. 3c, Table 2), while individuals of *Oenanthe lachenalii* tended to be taller in the monoculture plots ($p = 0.06$, Fig. 3d, Table 2).

3.3. Survival and performance of translocated populations

By the 1st season (Fig. 4, Table 3) between 56% and 100% of the introduced individuals per species had survived and by the 2nd season between 41% and 97% of the introduced individuals per species had survived, indicating that all translocations showed a promising short-term establishment. After the 2nd season we found flowering individuals in the translocated populations of *Ludwigia palustris* (37%), *Oenanthe lachenalii* (65%) and *Senecio erraticus* (3%) (Table 3).

By the 3rd season, four of the translocated populations had a population performance between 28% and 78% (*Senecio erraticus*, *Campanula cervicaria*, *Oenanthe lachenalii*, *Cleistogenes serotina*), while the other four populations had a population performance lower than 10% (*Allium angulosum*, *Ludwigia palustris*, *Teucrium scordium*, *Inula helvetica*; Fig. 4, Table 3). We found 30% of the individuals of *Campanula cervicaria* and 3.5% of the individuals of *Cleistogenes serotina* flowering (Table 3) and observed some clonal propagation in the translocated populations of *Cleistogenes serotina* and *Senecio erraticus*.

By the 4th season, *Campanula cervicaria* had a population performance of 28% and *Senecio erraticus* had a population performance of 39% (Fig. 4, Table 3). Due to clonal propagation *Cleistogenes serrotina* now had an increased population size

Table 2
Outcome of linear mixed effect models testing for the effect of genetic diversity (monoculture plots vs. mixture plots). Effects on survival, plant height and flowering of experimentally translocated individuals of eight threatened plant species. In the models over all species, we included time since transplantation as a covariate and genotype, species and plot identity as random terms (see example of R code in Appendix A3). In the single species models, we included seed family and plot identity as random terms. Estimates are given for the significant and marginally significant terms only. Additionally, p-values, degrees of freedom (df) and Chi square (χ^2) are given for each of the model's outputs.

		Mean survival rate				Plant height				Flowering			
		Estimate	p-value	df	χ^2	Estimate	p-value	df	χ^2	Estimate	p-value	df	χ^2
1st season	Over all species	**0.67**	**0.03**	**1**	**5.01**	–	0.48	1	0.50	–	–	–	–
	Allium angulosum	0.79	0.07	1	3.34	–	0.60	1	0.28	–	–	–	–
	Campanula cervicaria	–	0.15	1	2.01	–	0.17	1	1.86	–	–	–	–
	Cleistogenes serotina	–	0.24	1	1.40	**0.23**	**0.03**	**1**	**4.60**	–	–	–	–
	Ludwigia palustris	–	0.56	1	0.35	–	–	–	–	–	–	–	–
	Inula helvetica	–	0.60	1	0.28	–	–	–	–	–	–	–	–
	Oenanthe lachenalii	–	–	–	–	–	0.57	1	0.32	–	–	–	–
	Senecio erraticus	–	1.00	1	0.00	–	0.11	1	2.63	–	–	–	–
	Teucrium scordium	–	–	–	–	–	–	–	–	–	–	–	–
2nd season	Over all species	–	0.34	1	0.90	–	0.65	1	0.20	–	–	–	–
	Allium angulosum	–	0.24	1	1.38	–	0.51	1	0.43	–	–	–	–
	Campanula cervicaria	–	0.76	1	0.09	–	0.46	1	0.55	–	–	–	–
	Cleistogenes serotina	–	0.52	1	0.42	–	0.71	1	0.14	–	–	–	–
	Ludwigia palustris	–	0.34	1	0.92	–	0.67	1	0.18	–	0.92	1	0.01
	Inula helvetica	–	0.68	1	0.17	0.41	0.10	1	2.74	–	–	–	–
	Oenanthe lachenalii	–	–	–	–	−4.40	0.06	1	3.61	–	0.25	1	1.30
	Senecio erraticus	–	0.70	1	0.15	–	0.88	1	0.02	–	–	–	–
	Teucrium scordium	–	1.00	1	0.00	–	0.76	1	0.09	–	–	–	–

with a population performance of 250% (Fig. 4, Table 3). We found 12% of the individuals of *Campanula cervicaria*, 15% of the individuals of *Cleistogenes serotina* and 6% of the individuals of *Oenanthe lachenalia* flowering (Table 3).

4. Discussion

4.1. Relevance of high genetic diversity

Initially, plants growing in plots of higher genetic diversity survived better than plants growing in plots of lower genetic diversity. This is in line with general considerations on ecological consequences of genetic diversity (Hughes et al., 2008, Godefroid et al., 2016; Barmentlo et al., 2018) and it is consistent with the existing literature on the effect of genotypic variation on establishment success (Vergeer et al., 2005; Forsman, 2014; Prati et al., 2016). Higher genetic diversity is expected to increase the probability of having genotypes adapted to different biotic and abiotic conditions (sampling effect). It may also lead to increased resistance to enemies such as herbivores and pathogens (Zhu et al., 2000; Tooker and Frank, 2012) or decreased intraspecific competition for resources between different genotypes (complementarity effect, Loreau and Hector, 2001). The latter two mechanisms might have caused the positive diversity effect on survival that we found in the very first stage of our translocations shortly after planting, where stresses due to transplantation such as drought, root disturbance, abiotic differences, or the encountering of new enemies such as herbivores and pathogens can be particularly drastic (South and Zwolinski, 1997). We showed that genetic diversity can enhance the survival of translocated populations, however, this effect might only occur at particularly stressful stages, in our case the early stage of a translocation. Accordingly, Prati et al. (2016) found a positive effect of genetic diversity on translocated populations of *Ranunculus reptans* only after a severe flood, in this case several years after the translocation.

In the 2nd season of our experiment, the effect of genetic diversity disappeared, suggesting that other factors such as propagule pressure, habitat suitability or environmental stochasticity might be more important for the mid-term to longer-term survival of translocated plant populations. Nevertheless, high genetic diversity seemed to be important for the immediate survival after transplantation, and it is expected to become particularly important at even longer time scales once the consequences of longer-term evolutionary processes become apparent (Vergeer et al., 2005; Weeks et al., 2011). Future studies should therefore monitor the introduced populations as long as possible to disentangle the relative importance of a high number of founder individuals and genetic diversity on translocation success.

Plant height, which we measured as an additional parameter is often used as an indicator of plant fitness as being tall is correlated with a high biomass production and associated with high fecundity (Cornelissen et al., 2003). On the other hand, a greater height might indicate stronger competition for light (Falster and Westoby, 2003; Schmitt et al., 2003; Grundman et al., 2017). In our study, over all species, height was not affected by genetic diversity. For the individual species, we found mixed effects of genetic diversity on height. *Cleistogenes serotina* and *Inula helvetica* had taller plant individuals in mixture plots than in monoculture plots, either indicating better plant performance or increased intraspecific competition for light. In contrast, *Oenanthe lachenalii* had smaller individuals in mixture plots than in monoculture plots, either indicating poorer performance or reduced intraspecific competition for light. To assess plant performance more precisely, other components of fitness would

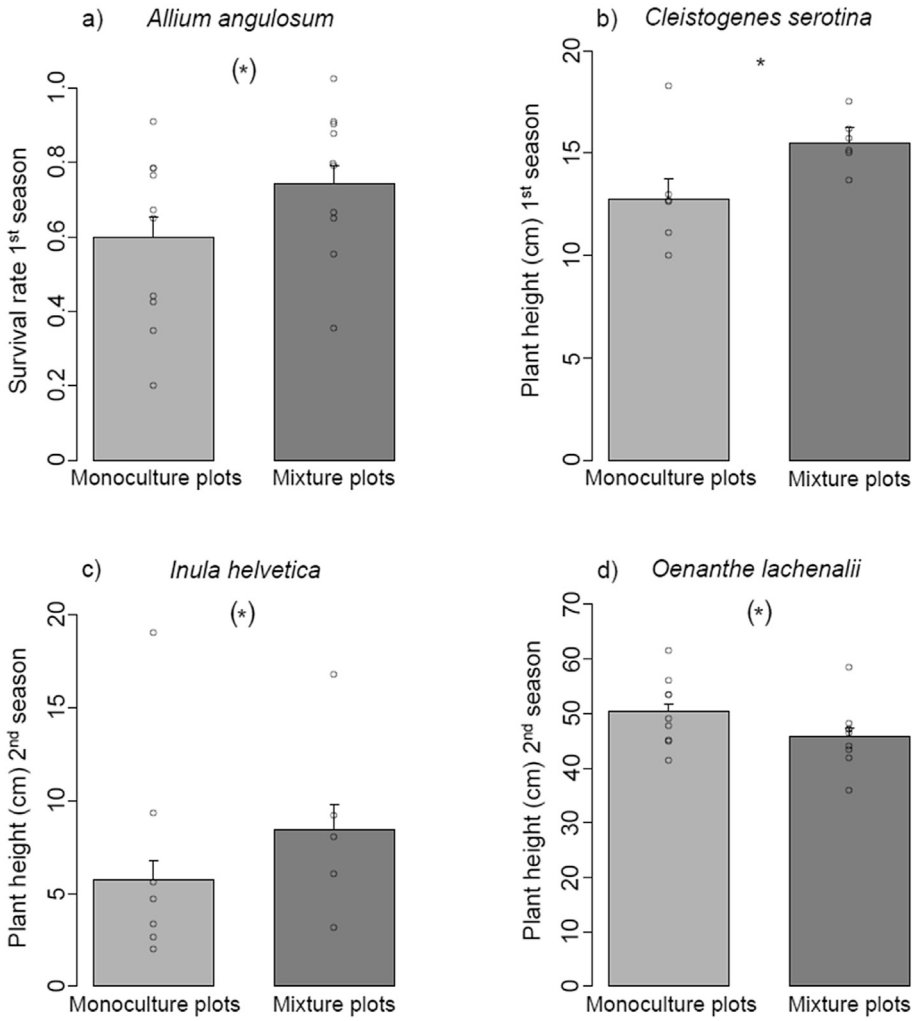


Fig. 3. Significant species-specific effects of genetic diversity. Effects on mean survival rate and height in monoculture (offspring of one seed family, light grey bars) and mixture plots (offspring of several seed families, dark grey bars) for the species showing a significant or marginally significant effect of genetic diversity on survival rate or plant height. Each dot represents the mean value for a single plot. The error bars represent the standard errors.

need to be measured, such as biomass or seed production (e.g. Younginger et al., 2017; Richman et al., 2020). However, as we did not want to interfere with the translocated plants, we refrained from taking destructive measures.

The strength of the diversity effect on survival in the first year differed between species, partly because mortality in some species (*Teucrium scordium*, *Oenanthe lachenalii*) was too low to show any effect of genetic diversity. It may also be that differences in the strength of the genetic diversity effect reflects differences in genetic variation between source populations of our species. For example, for very rare species with very small, isolated or declining populations, monoculture and mixture plots may hardly differ from each other, because the sampled genotypes may be genetically very similar (Gaston, 2006; Leimu et al., 2006). Species characteristics may also affect the genetic diversity of a population. For example, populations of species that propagate clonally are likely to be genetically less diverse than populations who do not propagate clonally (Ottewell et al., 2016). In our experiment, the strength of the diversity treatment was not related to the size of the populations from which seeds were collected, and it was also not related to the ability of clonal propagation or to the threat status of the species in Switzerland (Table A3). However, with only eight species (and less for some analyses, see Table A3) we were very limited in our ability to detect the factors driving variation in the strength of diversity effects. We suggest that future studies should take into account life history traits and population characteristics for many rare and threatened plant species to quantify the importance of population and species-specific characteristics (e.g. population size, life form, pollination system) on translocation success more thoroughly.

We did not measure genetic diversity of the source populations and of our maternal plants and can therefore only assume that plots with individuals from several maternal plants have a higher genetic diversity than plots with individuals of only one

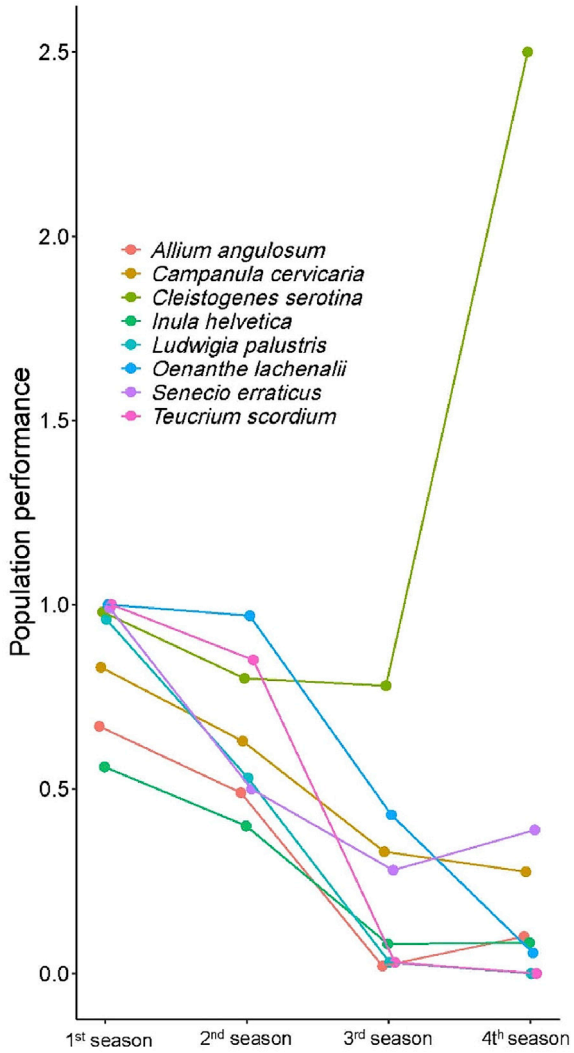


Fig. 4. Mean population performance (number of individuals **counted relative to the number of individuals planted) of the eight rare plant species over the four measurements.** 1st season was two months after the translocations, 2nd season was seven to ten months after the translocations, 3rd season was two years after the translocations and 4th season was three years after the translocation.

Table 3
Results of the experimental translocation of plants of eight rare species, each into a different field site. Population performance: number of individuals counted during monitoring/number of introduced individuals; Height: mean plant height in cm; Flowering: number of flowering individuals of the translocated populations in the 1st, 2nd, 3rd and 4th season of the experiment.

Species	1st season			2nd season			3rd season		4th season	
	Performance	Height	Flowering	Performance	Height	Flowering	Performance	Flowering	Performance	Flowering
Allium angulosum	0.67	4.9	0	0.49	7.8	0	0.02	0	0.1	0
Campanula cervicaria	0.83	6.3	0	0.63	13.7	0	0.33	30	0.28	12
Cleistogenes serotina	0.98	14.1	0	0.8	7.1	0	0.78	2	2.5	15
Inula helvetica	0.56	NA	0	0.41	7	0	0.08	0	0.08	0
Ludwigia palustris	0.96	NA	0	0.53	2.7	66	0.03	0	0	NA
Oenanthe lachenalii	1	3.5	0	0.97	48	93	0.43	NA	0.06	6
Senecio erraticus	0.99	17.4	0	0.5	23	5	0.28	0	0.39	0
Teucrium scordium	1	NA	0	0.85	3.8	0	0.03	0	0	NA

maternal plant. Since we found several diversity effects this indicates that the difference between our diversity treatments was large enough to test for an effect of genetic diversity, at least for most species. Thus, although we might have underestimated the importance of genetic diversity in our study, as all our species were threatened species (and their genetic

diversity may generally be lower than in common species, Gaston, 2006; Ottewell et al., 2016), the fact that we still found a positive effect of genetic diversity in the very first stage of establishment underlines the importance of using genetically diverse plant material for translocations. Genetic diversity is likely to become even more important in the long-term when recruitment starts to take place (Krauss et al., 2002; Weeks et al., 2011; Ottewell et al., 2016). Translocations of threatened plant species should therefore always try to maximise the genetic diversity of the source material.

4.2. Translocation of rare and threatened plant species

The translocation of threatened plant species has become an increasingly important conservation method. Unfortunately, several studies show that translocations are often not successful. In a meta-analysis including 249 plant translocations, Godefroid et al. (2011) assessed a mean survival rate over all translocations included in their study of approximately 52% and a flowering rate over all translocations of about 19% after one year, and a further decrease of survival and flowering rate with time. Further, Drayton and Primack (2012) found in their study that six out of eight introduced species had died after 15 years. In our study, all eight translocated populations were still alive one year after the translocation with a survival rate from 41% to 97%, and three translocated populations had flowering individuals. After two years, in four out of the eight translocated populations most individuals had died (survival rate < 10%), most likely due to the exceptionally dry summer in 2015, where sites, which are normally occasionally flooded, fell dry during the whole year (*Allium angulosum, Ludwigia helvetica, Teucrium scordium*) and did not meet the species requirements any more. Two species suffered from intensive perturbations, grazing by wildlife immediately after planting (*Allium angulosum*) or soil erosion from water running over the plot (*Inula helvetica*). Nevertheless, four out of eight translocated populations still had a survival rate between 28% and 78% after two years, and out of those, three translocated populations had flowering individuals or vegetative propagation. Lastly, after three years one population had increased its population size compared with the initially planted individuals due to intensive clonal propagation by a factor of 2.5 (*Cleistogenes serotine*) and two other populations still had a survival rate of 28% (*Campanula cervicaria*) and 39% (*Senecio erraticus*). In addition to the one species showing an increased population growth, two species showed positive trends after a strong initial population decline (*Senecio erraticus*, *Allium angulosum*). These observations reflect the difficulties of meeting habitat requirements of translocated species and highlight the importance of introducing a large number of individuals and translocations at multiple sites and microsites or over several years to overcome environmental stochasticity such as extreme weather events or disturbances (see also Dunwiddie and Martin, 2016; Silcock et al., 2019; Caughlin et al., 2019). Due to our focus on a test of the general importance of genetic diversity, we translocated fewer plant individuals (40–312 per site) than is recommended in Switzerland (at least 500, Info Flora, 2016). Nevertheless, our results also reflect that combining population biological knowledge and botanical expert knowledge on species and habitats of threatened species can be promising. We suggest that future plant translocations should be accompanied by both scientists and practitioners to comprehensively address questions on species biology, habitat suitability, choice of a large sample sizes and genetic material of founder individuals, high number of introduced individuals, transplant design and data analysis. Bridging the gap between scientists and practitioners, combined with long-term monitoring of population growth, allows to disentangle the relative importance of the various factors driving translocation success of rare and threatened plant species.

5. Conclusion

Our study shows that a higher genetic diversity generally enhances the short-term survival of translocated populations. This highlights the importance of using genetically diverse plant material for the translocation of rare and threatened plant species. Our study also demonstrates the power of experimental approaches in conservation. We therefore recommend close collaborations between experimental plant ecologists, field botanists and conservation practitioners at all stages of translocations, during species and site selection, when designing and setting up experiments and during monitoring. Only scientifically assisted long-term translocation experiments will enable us to disentangle the role of different potentially important factors for translocation success and therefore to enhance our understanding of these underlying factors for the success or failure of translocations of threatened plant species. This will help us to make translocations of species and assisted migration a promising tool to face the decline of biodiversity under ongoing global change.

Funding

This work was supported by the Federal office for the Environment (FOEN).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

We thank Info Flora (Bern and Geneva, Switzerland) and the Botanical Garden of the University of Bern for their practical support and their advice concerning regulations, and all federal and cantonal authorities, conservation experts, and botanists for their collaboration. We also thank Judith Hinderling, Karl Kasper, Yvonne Küenzi, Stefan Blaser, Armin Komposch, Janique Bertschi and Judith Minker for their help in the field, and Daniel Prati and Eric Allan for their help with the analyses. We also thank three anonymous reviewers for their constructive and helpful comments. We thank the Swiss Federal Office for the Environment for financial support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01240.

Appendix

Table A1
List of the origins of the study species and the translocation locations. The abbreviations stand for different cantons in Switzerland, BE = Bern, GE = Genève, TI = Ticino, VD = Vaud, VS = Valais, ZH = Zürich.

Species	Seed origin	Size of source population	Year of seed collection	Location of translocation
Allium angulosum	Mörigenbucht, BE	>1000	2012	Mörigenbucht, BE
Campanula cervicaria	Chlosteralp und Forst, BE	50–100	2012	Chlosteralp, BE
Cleistogenes serotina	Ayent, VS	<50	2011	Aven, VS
Inula helvetica	Aeust am Albis, ZH	>1000	2012	Thürlerseegebiet, ZH
Ludwigia palustris	Bolle di Magadino, TI	>1000	2011	Verzasca Delta, TI
Oenanthe lachenalii	Au, ZH	50–200	2011	Au, ZH
Senecio erraticus	Aire-La-Ville, GE	~200	2012	Commugny, VD
Teucrium scordium	Plaine des l'Orbe, VD	>1000	2012	NSG Häftli, BE

Table A2
Details on the design of the experimental species translocations

Species	Number of seed families	Number of plots	Number of individuals per plot	Total number of translocated individuals
Allium angulosum	10	20	9	180
Campanula cervicaria	13	26	12	312
Cleistogenes serotina	6	12	5	60
Inula helvetica	7	14	6	84
Ludwigia palustris	10	20	9	180
Oenanthe lachenalii	9	18	8	144
Senecio erraticus	10	20	9	180
Teucrium scordium	5	10	4	40

A3: Supplementary material and methods: R code of the statistical model testing for treatment effects for a) single species and b) over all species.
a)m1<-glmer(survival ~ treatment + (1|seedfamily) + (1|plot), data = dataspecies, family = binomial) m2<-glmer (survival ~ (1| seedfamily) + (1|plot), data = dataspecies, family = binomial) anova(m1, m2).
b)m1 <- lmer (survival ~ growing_period + treatment + (1|species/seedfamily) + (1|plot), data = dataall, family = binomial) m2 <- lmer (survival ~ growing_period + (1|species/seedfamily) + (1|plot), data = dataall, family = binomial) anova(m1, m2).

Table A3
Output of linear models analysing the influence of the size of the source populations, status of threat and the ability of vegetative propagation of the study species on the strength of the diversity effect (estimate for diversity) in first and second season survival and plant height. Due to the low number of species (replicates), we analysed each explanatory variable in a separate model. Given are the Estimates, standard errors, F-values, p-values and the degrees of freedom (DF1 (response variable) and DF2 (residuals)). For survival, we excluded species from the analysis that did not show any mortality or were only one individual died (as we considered this to be potentially also chance). Note, that the number of species is therefore very limited to draw broad and general conclusions.

	1st season					2nd season				
	Treatment effect for mean survival rate					Treatment effect for mean survival rate				
	Estimates	Standard error	F-value	p-value	DF1/DF2	Estimates	Standard error	F-value	p-value	DF1/DF2

Table A3 (*continued*)

	1st season					2nd season				
	Treatment effect for mean survival rate					Treatment effect for mean survival rate				
	Estimates	Standard error	F-value	p-value	DF1/DF2	Estimates	Standard error	F-value	p-value	DF1/DF2
Source population size	0.001	0.000	4.236	0.132	1/3	0.000	0.000	1.774	0.240	1/5
Red List status (CH)	0.212	0.261	0.661	0.476	1/3	−0.211	0.184	1.326	0.302	1/5
Vegetative propagation	−0.039	0.441	0.008	0.934	1/3	−0.375	0.273	1.883	0.228	1/5
	Treatment effect for plant height					Treatment effect for plant height				
	Estimates	Standard error	F-value	p-value	DF	Estimates	Standard error	F-value	p-value	DF
Source population size	−0.001	0.002	0.325	0.609	1/3	0.001	0.001	1.274	0.302	1/6
Red List status (CH)	0.807	0.650	1.540	0.303	1/3	1.061	0.671	2.501	0.165	1/6
Vegetative propagation	0.781	1.135	0.473	0.541	1/3	−0.497	1.426	0.121	0.740	1/6

References

Barmentlo, S.H., Meirmans, P.G., Luijten, S.H., Triest, L., Oostermeijer, J.G.B., 2018. Outbreeding depression and breeding system evolution in small, remnant populations of Primula vulgaris: consequences for genetic rescue. Conserv. Genet. 19, 545–554. https://doi.org/10.1007/s10592-017-1031-x.

Bates, D.B., Mächler, M., Bolker, B., Walker, S., 2015. Package Lme4: Linear mixed-effect models using eigen and S4. R package version 67.

Bornand, C., Eggenberg, S., Gygax, A., Juillerat, P., Jutzi, M., Rometsch, S., et al., 2016. Liste rouge Plantes vasculaires: espèces menacées en Suisse. With assistance of OFEV, DETEC, Info Flora. OFEV, Bern.

Caughlin, T.T., Damschen, E.I., Haddad, N.M., Levey, D.J., Warneke, C., Brudvig, L.A., 2019. Landscape heterogeneity is key to forecasting outcomes of plant reintroductions. Ecol. 29 (2), e01850 https://doi.org/10.1002/eap.1850.

Charlesworth, D., Charlesworth, B., 1987. Inbreeding depression and its evolutionary consequences. Annu. Rev. Ecol. Systemat. 18 (1), 237–268. https://doi.org/10.1146/annurev.es.18.110187.001321.

Cornelissen, J., Lavorel, S., Garnier, E.B., Diaz, S., Buchmann, N., Gurvich, D., et al., 2003. Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51, 335–380. https://doi.org/10.1071/BT02124.

Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. Annu. Rev. Environ. Resour. 28, 137–167. https://doi.org/10.1146/annurev.energy.28.050302.105532.

Drayton, B., Primack, R.B., 2012. Success rates for reintroductions of eight perennial plant species after 15 years. Restor. Ecol. 20 (3), 299–303. https://doi.org/10.1111/j.1526-100X.2011.00860.x.

Dunnwiddie, P.W., Martin, R.A., 2016. Microsites matter: improving the success of rare species reintroductions. PloS One 11 (3), e0150417. https://doi.org/10.1371/journal.pone.0150417.

Ellstrand, N.C., Elam, D.R., 1993. Population genetic consequences of small population size: implications for plant conservation. Annu. Rev. Ecol. Systemat. 24 (1), 217–242. https://doi.org/10.1146/annurev.es.24.110193.001245.

Falster, D.S., Westoby, M., 2003. Plant height and evolutionary games. Trends in Ecology & Evolution 18 (7), 337–343. https://doi.org/10.1016/S0169-5347(03)00061-2.

Fischer, M., Matthies, D., 1998. Effects of population size on performance in the rare plant Gentianella germanica. J. Ecol. 86 (2), 195–204. https://doi.org/10.1046/j.1365-2745.1998.00246.x.

FOEN, 2011. List of Priority Species at the National Level. Bern, Switzerland.

Forsman, A., 2014. Effects of genotypic and phenotypic variation on establishment are important for conservation, invasion, and infection biology. Proc. Natl. Acad. Sci. Unit. States Am. 111 (1), 302–307. https://doi.org/10.1073/pnas.1317745111.

Frankham, R., Ballou, J.D., Briscoe, D.A., 2010. Introduction to Conservation Genetics. Cambridge University Press, Cambridge.

Gamfeldt, L., Källström, B., 2007. Increasing intraspecific diversity increases predictability in population survival in the face of perturbations. Oikos 116 (4), 700–705. https://doi.org/10.1111/j.0030-1299.2007.15382.x.

Gaston, K.J., 2006. The Structure and Dynamics of Geographic Ranges. Oxford University Press, Oxford (Oxford Series in Ecology and Evolution).

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.-D., Aguraiuja, R., et al., 2011. How successful are plant species reintroductions? Biol. Conserv. 144 (2), 672–682. https://doi.org/10.1016/j.biocon.2010.10.003.

Godefroid, S., Le Pajolec, S., Van Rossum, F., 2016. Pre-translocation considerations in rare plant reintroductions: implications for designing protocols. Plant Ecol. 217, 169–182. https://doi.org/10.1007/s11258-015-0526-0.

Godt, M.J.W., Johnson, B.R., Hamrick, J.L., 1996. Genetic diversity and population size in four rare southern appalachian plant species. Conserv. Biol. 10 (3), 796–805. https://doi.org/10.1046/j.1523-1739.1996.10030796.x.

Grundtman, M., Gross, D., Màjekovà, M., Tielbörger, K., 2017. Decision-making in plants under competition. Nat. Commun. 8, 2235. https://doi.org/10.1038/s41467-017-02147-2.

Hughes, A., Randall, I., Brian, D., Johnson, M.T.J., Underwood, N., Vellend, M., 2008. Ecological consequences of genetic diversity. Ecol. Lett. 11 (6), 609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x.

IPBES, Fischer, M., Rounsevell, M., Torre-Marin Rando, A., Mader, A., Church, A., Elbakidze, M., et al., 2018. Summary of Policymakers of the Regional Assessment Report on Biodiversity and Ecosystem Services for Europe and Central Asia of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. With Assistance of. IPBES secretariat, Bonn, Germany.

IUCN/SSC, 2013. Guidelines for Reintroductions and Other Conservation Translocations. Version 1.0. IUCN Species Survival Commission, Gland, Switzerland, ISBN 978-2-8317-1609-1 viiii + 57.

IUCN/SSC, 2014. Guidelines on the Use of Ex Situ Management for Species Conservation. IUCN Species Survival Commission, Gland, Switzerland. Version 2.0.

Jump, A.S., Mátyás, C., Peñuelas, J., 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends Ecol. Evol. 24 (12), 694–701. https://doi.org/10.1016/j.tree.2009.06.007.

Krauss, S.L., Dixon, B., Dixon, K.W., 2002. Rapid genetic decline in a translocated population of the endangered plant *Grevillea scapigera*. Conserv. Biol. 16 (4), 986–994. https://doi.org/10.1046/j.1523-1739.2002.01105.x.

Landolt, E., Bäumler, B., 2010. Flora indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. 2., völlig neu bearbeitete und erweiterte Auflage der Ökologischen Zeigerwerte zur Flora der Schweiz, 1977. Bern, Haupt.

Lauber, K., Wagner, G., Gygax, A., 2012. Flora Helvetica. Haupt Verlag, Bern, ISBN 978-3-258-07700-0.

Leimu, R., Mutikainen, P.I.A., Koricheva, J., Fischer, M., 2006. How general are positive relationships between plant population size, fitness and genetic variation? J. Ecol. 94 (5), 942–952. https://doi.org/10.1111/j.1365-2745.2006.01150.x.

Lesica, P., Allendorf, F.W., 1999. Ecological genetics and the restoration of plant communities: mix or match? Restor. Ecol. 7 (1), 42–50. https://doi.org/10.1046/j.1526-100X.1999.07105.x.
Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature 412 (6842), 72–76. https://doi.org/10.1038/35083573.
Maschinski, J., Haskins, K.E., Raven, P.H., 2012. Plant Reintroduction in a Changing Climate. Island Press/Centre for Resource Economics, Washington, DC.
Maunder, M., 1992. Plant reintroduction: an overview. Biodivers. Conserv. 1 (1), 51–61. https://doi.org/10.1007/BF00700250.
Mayr, E., 1963. Animal Species and Evolution. Harvard University Press, Cambridge, Mass.
Menges, E.S., 2008. Restoration demography and genetics of plants: when is a translocation successful? Aust. J. Bot. 56 (3), 187. https://doi.org/10.1071/BT07173.
Moser, D.M., Gygax, A., Bäumler, B., Wyler, N., Palese, R., 2002. Rote Liste der gefährdeten Arten der Schweiz: Farn- und Blütenpflanzen. With assistance of ZDSF, CJBG, BUWAL. Bern (Eds.). With assistance of ZDSF, CJBG, BUWAL, VU-9006-D.
Noël, F., Prati, D., van Kleunen, M., Gygax, A., Moser, D., Fischer, M., 2011. Establishment success of 25 rare wetland species introduced into restored habitats is best predicted by ecological distance to source habitats. Biol. Conserv. 144 (1), 602–609. https://doi.org/10.1016/j.biocon.2010.11.001.
Oostermeijer, J.G.B., van Eijck, M.W., den Nijs, J.C.M., 1994. Offspring fitness in relation to population size and genetic variation in the rare perennial plant species Gentiana pneumonanthe (Gentianaceae). Oecol 97 (3), 289–296. https://doi.org/10.1007/BF00317317.
Ottewell, K.M., Bicherton, D.C., Byrne, M., Lowe, A.J., 2016. Bridging the gap: a genetic assessment framework for population-level threatened plant conservation prioritization and decision-making. Divers. Distrib. 22, 174–188. https://doi.org/10.1111/ddi.12387.
Ouborg, N.J., van Treuren, R., 1994. The significance of genetic erosion in the process of extinction. IV. Inbreeding load and heterosis in relation to population size in the mint salvia pratensis. Evolution 48 (4), 996–1008. https://doi.org/10.1111/j.1558-5646.1994.tb05288.x.
Prati, D., Peintinger, M., Fischer, M., 2016. Genetic composition, genetic diversity and small-scale environmental variation matter for the experimental reintroduction of a rare plant. Plant Ecol. 9 (6), 805–813. https://doi.org/10.1093/jpe/rtv067.
Price, M.V., Waser, N.M., 1979. Pollen dispersal and optimal outcrossing in Delphinium nelsoni. Nature 277 (5694), 294–297. https://doi.org/10.1038/277294a0.
R Core Team, 2016. R: A language and environment for statistical computing.. R Foundation for statistical computin, Vienna, Austria.
Richman, S.K., Levine, J.M., Stefan, L., Johnson, C.A., 2020. Asynchronous range shifts drive alpine plant-pollinator interactions and reduce plant fitness. Global Change Biol. 26, 3052–3064. https://doi.org/10.1111/gcb.15041.
Sala, O.E., 2000. Global biodiversity scenarios for the year 2100. Science 287 (5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770.
Schmitt, J., Stinchcombe, J.R., Heschel, M.S., Huber, H., 2003. The adaptive evolution of plasticity: phytochrom-mediated shade avoidance reponses. Integr. Comp. Biol. 43, 459–469. https://doi.org/10.1093/icb/43.3.459.
Silcock, J.L., Simmons, C.L., Monks, L., Dillon, R., Reiter, N., Jusaitis, M., et al., 2019. Threatened plant translocation in Australia: a review. Biol. 236, 211–222. https://doi.org/10.1016/j.biocon.2019.05.002.
South, D.B., Zwolinski, J.B., 1997. Transplant Stress Index: a proposed method of quantifying planting check. New Forest 13 (1–3), 315–328. https://doi.org/10.1023/A:1006546627342.
Taberlet, P., Zimmermann, N.E., Englisch, T., Tribsch, A., Holderegger, R., Alvarez, N., et al., 2012. Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. Ecol. Lett. 15 (12), 1439–1448. https://doi.org/10.1111/ele.12004.
Tooker, J.F., Frank, S.D., 2012. Genotypically diverse cultivar mixtures for insect pest management and increased crop yields. J. Appl. Ecol. 49 (5), 974–985. https://doi.org/10.1111/j.1365-2664.2012.02173.x.
Vergeer, P., van den Berg, L.J.L., Roelofs, J.G.M., Ouborg, N.J., 2005. Single-family versus multi-family introductions. Plant Biol. 7 (5), 509–515. https://doi.org/10.1055/s-2005-865904.
Vergeer, P., Sonderen, E., Ouborg, N.J., 2004. Introduction strategies put to the test: local adaptation versus heterosis. Conserv. Biol. 18 (3), 812–821. https://doi.org/10.1111/j.1523-1739.2004.00562.x.
Weeks, A.R., Sgro, C.M., Young, A.G., Frankham, R., Mitchell, N.J., Miller, K.A., et al., 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evol. Appl. 4, 709–725. https://doi.org/10.1111/j.1752-4571.2011.00192.x.
Wolf, C.M., Griffith, B., Reed, C., Temple, S.A., 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conserv. Biol. 10 (4), 1142–1154. https://doi.org/10.1046/j.1523-1739.1996.10041142.x.
Younginger, B.S., Sirovà, D., Cruzan, M.B., Ballhorn, D.J., 2017. Is biomass a reliable estimate of plant fitness? Appl. Plant Sci. 5 (2), 1600094. https://doi.org/10.3732/apps.1600094.
Zavodna, M., Abdelkrim, J., Pellissier, V., Machon, N., 2015. A long-term genetic study reveals complex population dynamics of multiple-source plant reintroductions. Biol. Conserv. 192, 1–9. https://doi.org/10.1016/j.biocon.2015.08.025.
Zeng, X.Q., Durka, W., Fischer, M., 2017. Species-specific effects of genetic diversity and species diversity of experimental communities on early tree performance. Plant Ecol. 10, 252–258. https://doi.org/10.1093/jpe/rtw108.
Zhu, Y., Chen, H., Fan, J., Wang, Y., Li, Y., Chen, J., et al., 2000. Genetic diversity and disease control in rice. Nature 406 (6797), 718–722. https://doi.org/10.1038/35021046.